VII. *Lapworthura: a Typical Brittlestar of the Silurian Age; with Suggestions for a New Classification of the Ophiuroidea.*

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[PLATES 9 AND 10.]

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The anatomy of the Palæozoic Ophiuroidea has been far from exhaustively studied, though they possess features of great interest. The nature of the available material and the impossibility of obtaining conclusive evidence by the older methods of study are sufficient reasons for our imperfect knowledge of these primitive organisms.

In the following paper an account is given of the structure of the Silurian Ophiurid *Lapworthura miltoni* (Salter), based upon a study of the fine series of this fossil in the Oxford Museum and of models made by the method described by one of us in 1901 (23), 1903 (24); other Palæozoic Ophiuroidea are described and compared with Lapworthura, and the bearing of the facts upon the interpretation of the structure of modern types is considered.

It will be seen that in all essential points Lapworthura conforms to the type of structure discovered by JAEKEL in Eophiura, Palæura, and Bohemura (11), though it has reached a more advanced stage of evolution. And indeed there is evidence to show that all the Silurian and Devonian Ophiurids possess a fundamentally similar structure. It is not possible to give exact detailed descriptions of all the named genera, but it is not difficult, in the light of the knowledge gained from the study of Lapworthura, to recognise in them a natural group differing in important respects from existing forms. It follows from this that a revision of the classification of Ophiuroidea is necessary.

Carboniferous Brittlestars have been described by MEEK and WORTHEN (18). The description of their genus Onychaster is not very complete but is sufficient to

show that in the Carboniferous era an advanced stage of evolution had been reached by this form; and whether, as MEEK and WORTHEN'S description would lead us to suppose, this form is extremely aberrant, or whether it approximates in structure to modern types, as SCHÖNDORF maintains, in either case its existence in the Carboniferous epoch precludes the division of the Ophiuroidea into Palæophiuroidea and Neophiuroidea, but we suggest the formation of a group Protophiuroidea for the Silurian and Devonian forms characterised by the completeness of the ambulacral series (the first pair of ambulacral ossicles (a_1) being retained), by the meeting of the ambulacral series of adjacent arms on the abactinal side of the jaws, and by the absence of upper and under arm-plates.

All the modern genera form a group Euophiuroidea, characterised: (1) by the specialised buccal armature consisting of oral angle pieces formed by the complete fusion of a_2 and ad_1, a_1 having been lost; (2) by the presence of under arm-plates, with the single exception of Ophioteresis.

With regard to the systematic position of Onychaster we refrain from offering an opinion till our own investigations are completed.

Eucladia has already been assigned to a special group, the Ophiocistia (25), which is here retained but raised to the rank of a class equal in value to the Ophiuroidea, and possibly more nearly allied to them than to any other class of the Echinodermata.

Description of Lapworthura miltoni (*Salter*).*

This species was first described by SALTER in 1857, under the name of *Protaster miltoni*, and re-described by him in 1861 (20). In his second paper SALTER came to the conclusion that the madreporite is abactinal (dorsal), and this led him to consider that *Protaster miltoni* should be transferred from the Ophiuroidea to the Asteroidea, its resemblance to the former group being merely imitative. He gave a figure correct as far as it went (Plate 18) representing the "real shape of the ambulacral bones." In 1886 STÜRTZ restored this species to the Ophiuroidea (26).

In 1896 GREGORY (9) created the genus Lapworthura for *Protaster miltoni*. He gave a new figure of the arm skeleton, in which the anterior end of the ambulacral ossicles is incorrectly represented as the posterior. He followed SALTER in assigning the madreporite to the abactinal surface, and endeavoured to show that this is the primitive position of the madreporite in the class. GREGORY'S statements influenced the views of STÜRTZ. In 1890 STÜRTZ had suggested that if the madreporite originally occurred on the same aspect of the body in both Starfish and Brittlestars, it was actinal in both and that it is in the Starfish and not in the Brittlestar that

* SCHÖNDORF'S work came to our notice only after the completion of the present paper. He has recognised, on the same evidence as our own, the true position of the madreporite. With his main contention that the ambulacral ossicles were hollow half-cylinders and that consequently Lapworthura and all other Protophiuroidea must be removed from the Ophiuroidea, we are unable to agree; on this point the evidence afforded by our sections leaves no room for doubt.

a change has taken place. He called attention to a prediction made by SLADEN (22) in 1880, who, commenting on AGASSIZ's statement (1) that in very young starfish the madreporite is at first ventral (actinal) and only subsequently becomes dorsal (abactinal), suggested that ancient fossil starfish would be found in which the madreporite retained its ventral (actinal) position in the fully adult state. STÜRTZ added that this prophetic remark had not had long to wait for justification; several fossil starfish were already known at that date in which the madreporite lies on the actinal surface of the adult.

In 1893 (28) STÜRTZ's views on this subject were unchanged. In 1900 he drew attention to the difficulty which is introduced into the phylogeny of Stelleroidea by GREGORY's description of Lapworthura and of Eucladia, and by his statements that BURY had found a dorsal madreporite in young Ophiuroidea; for, he argued, while in Starfish we have modern forms with a dorsal (abactinal) madreporite and primitive forms with ventral (actinal) madreporite, and according to AGASSIZ, a ventral (actinal) madreporite in young starfish, in the Ophiuroidea on the other hand the converse appears to be the case. Again, if in the original stock of Ophiuroidea the madreporite lay on the abactinal, and in the original stock of the Asteroidea on the actinal side, this fact would not lead to the view that the Ophiuroidea and Asteroidea were derived from the same stock. Here it should be pointed out that GREGORY was mistaken in his quotation of BURY, who was speaking not of the young Ophiuroid but of the larva. In the same year (1900) GREGORY in his article in LANKESTER's 'Treatise on Zoology,' while still apparently holding the view that the madreporite is "dorsal" (abactinal) in some Ophiuroidea (see p. 238), did not turn his attention to the phylogenetic importance of this character.

The argument from embryology is considerably altered by modern work and is by no means decisive. BURY's figures (4) of newly metamorphosed Asterid larvæ (Plate 6, figs. 21, 22, 24, *Bipinnaria asterigera*) show the water pore as marginal and actinal. MACBRIDE (15) describes the madreporite in young Amphiura as near the edge of the disc, and the stone canal as nearly horizontal. But he points out that "the arrangement in Amphiura might be obtained from that in Asterina by rotating the stone canal and accompanying structures outwards and downwards through an angle of 180°." He finds indications that this is what has actually occurred in the phylogeny, in the position of madreporite and stone canal of young Amphiura and in the undulating course of the genital rachis, which "points to the conclusion that the aboral parts of the inter-radii have greatly developed and have grown on to the oral surface . . . . and so the stone canal has been swung round . . . . In Asterina there is a trace of this process," and MACBRIDE is inclined to look on the condition of Asterina as the primitive one from which both Asterid and Ophiurid arrangements have been derived. But the evidence which he gives of the primitive nature of Asterina tends to prove only that it is primitive among Asterids.

It is clear then that position of the madreporite in Lapworthura is a matter of

importance and needs careful determination. It has already been shown by one of us (25) that the madreporite of Eucladia is actinal. An examination of the fine collection of *Lapworthura miltoni* in the Oxford Museum has convinced us that here, too, the madreporite occupies a position on the actinal surface. When well preserved there is no mistaking the nature of this structure ; it is situated inter-radially near one of the arms, within the region of the disc, is almost hemispherical in form, measures about 0·78 mm. in diameter, and is covered with a characteristic labyrinth of fine ridges. As to its recognition there can be no difficulty, but what is not so easy, on first studying the subject, is to determine which is the abactinal and which is the actinal aspect of the organism. The distribution of the integumentary remains of the disc is a criterion which at once suggests itself, but one tedious in application and more useful for confirmation than discovery. A much readier guidance is furnished by the arrangement of the plates of the buccal armature. Slight inspection suffices to arrange a collection of Lapworthura in two series, one in which the jaws originate within the arms, continuing the direction of the vertebral ossicles, and the other in which the oral framework prolongs the direction of the lateral plates ; an examination of any modern Ophiurid will suffice to show that a similar difference in the relations of the oral armature is presented, according as the dissected disc is viewed from the abactinal or actinal aspect : and the actinal surface is that on which the lateral buccal shields are exposed as a prolongation of the series of lateral arm-plates. This fact teaches that the second of the series into which we have supposed our collection of Lapworthura to be divided consists of specimens presenting the actinal aspect to view ; now it is on these and these only that the madreporite is found to occur. The madreporite is consequently actinal in position, a conclusion which the examination of the integumentary remains fully confirms.

It may further be added that the position of the madreporite is as nearly as possible that which it still occupies in most existing Brittlestars ; in almost all cases it lies side by side with the second or third adambulacral plate, sometimes in contact with the base of the first adambulacral, which enters into the oral framework. There are no oral plates in Lapworthura, but in the modern Brittlestars these scales cover precisely that part of the inter-radial area which corresponds to the angle in which the madreporite of the fossil is placed, while, to make the similitude more exact, the perforation of the oral plate by the stone canal in recent forms is always eccentric, and situated on the same side of the inter-radius as in Lapworthura. Had Lapworthura possessed oral plates, one of them would have inevitably surrounded the madreporite in the fashion characteristic of living Ophiurids.

The Skeleton of the Arms.—That the ambulacral ossicles are paired and opposite is well known, and it has been asserted by STÜRTZ, whose statement is confirmed by Dr. GREGORY, that they are fused in the median line. As this is a matter of some importance, it may be considered first. The notion of a union of the ambulacral ossicles is not suggested by an examination of either the actinal or abactinal surfaces

of the arm; a deep groove separates the adjacent ossicles on each face, and was doubtless occupied by a radial water vascular canal on the ventral side. The existence of these grooves does not prove conclusively that the ossicles were separate; the fact, however, that in some specimens a displacement of the ossicles has occurred, so that the members of a pair cease to be opposite, and become alternate in position is suggestive, and proves that, if any connection originally existed, it must have been of the slightest kind.

A few of the Leintwardine specimens are preserved, not as casts, but as solid calcareous residues, and these provided the material from which the models were made. In the case of transverse sections, the relations of the parts were fairly well shown, though their form had been greatly distorted by earth pressure. No evidence was obtained of any intimate union between the ambulacral ossicles. A welcome confirmation of the statement that upper and under arm-plates are absent in these Ophiurids was met with: the lateral arm-plates were seen bearing spines, and articulated with the ambulacral ossicles, but no trace of any other structures was visible in the surrounding matrix, although a great number of sections were observed. Horizontal sections gave similar results, the actinal and abactinal grooves are continued between the ossicles from one face to the other; ambiguous cases were sometimes encountered, which might suggest a union, but these are more probably explained as due to the obliteration of the original fissure by pressure.

The form of the ossicles is very different as they are viewed from the actinal or abactinal side; abactinally, they somewhat resemble the phalanges of a Plesiosaur, and are in contact at each end; they are slightly rounded from side to side in the middle, thickened at each extremity, and produced into curved lateral processes at the outer corners. On the actinal side they look somewhat like two capital letters "L" placed back to back; the base of the "L" is broad and thick, and affords an articular surface for the lateral plates; the limb is also wide, and immediately distal to the base is depressed, but further on becomes thicker; this thickened part is excavated by a deep groove, which extends obliquely outwards and backwards (in a proximal direction); the edges of this are sometimes obviously thickened; occasionally this groove is closed at the inner end, but more usually opens freely into the cavity of the arm. There can be little doubt that it received the branch of the radial water canal that supplied the tentacles. At its distal termination the leg of the "L" is depressed.

As the vertebral ossicles are traced from the oral end of the arm outwards, an interesting change may be remarked in their form; at first they are somewhat broader than long, but subsequently these relations are reversed. Thus a pair of ossicles situated about one-quarter of the length of an arm from its origin measured 1·3 mm. in length and 1·5 mm. in breadth, but at the broken extremity of the arm the breadth had diminished to 0·3 to 0·5 mm., while the length had been but slightly reduced, viz., to 1·1 mm.; in another instance, an ossicle viewed from the abactinal

side, at a point just outside the disc, had a length of 1·1 mm., while its breadth taken across the middle was 1·7 to 1·8 mm.; near the distal end of the arm an ossicle measured 1·7 mm. in length and 1·1 mm. in breadth. As the ossicles become narrower they also become simpler, and finally are reduced to mere cylindrical rods.

The modern growth of the science of embryology has opened up a wide field of interest in the comparison of ancient forms of life with early stages in the development of the individual, but the warning becomes ever more emphatic not to trust to embryology as a guide until its indications are checked by palæontology or comparative morphology. A striking parallel is afforded by the forms through which the vertebral ossicles of a recent Ophiurid pass in the course of their development, and those which succeed one another in the chronological series of their fossil predecessors. Thus, in existing species, one of the earliest forms of the vertebral ossicle is that of a simple rod, such as characterises a whole group of Palæozoic Ophiurids, and which is represented in the youngest ossicles in the arm of *Lapworthura miltoni*. In the next stage the ossicles of a modern species broaden out, and become united at their extremities, leaving a narrow bi-convex opening in the centre, which is strikingly similar in form to the interspace between the bodies of a pair of ossicles in Lapworthura, though these, as we have seen, are in all likelihood not yet united together. In the next stage of development in modern Ophiurids the ossicle becomes thicker and grows up about the branch of a water canal which supplies the tube feet, but does not at first wholly enclose it, or, in other words, a furrow is formed for the passage of the canal, resembling the furrow on the ventral side of the ossicles in Lapworthura. The raised lips of this furrow in the fossil form seem to be a step towards roofing it over.

The lateral plates take a large share in the skeleton of the arms, they are scarcely inferior in size to the ambulacral ossicles; each consists of a rod-like stem and a petal-like lamina; the lamina is curved in conformation with the exterior of the arm, it extends forwards and backwards the whole length of a segment, and articulates or overlaps in each direction with the similar plates next to it in the series; on its surface it bears a row of small granules with which the heads of the spines, four or five in number, are in contact. The end of the stem abuts on the proximal thickening of the ventral surface of a vertebral ossicle.

The absence of upper and under arm-plates has already been referred to, and it only remains to add that in modern Ophiurids these plates make a later appearance than the ambulacral and adambulacral ossicles. The difference in time of appearance is not great, being measured in the history of the young Brittlestar by days or even hours, though in the evolution of the race it was a matter of unknown æons.

Buccal Armature.—The buccal armature has hitherto received no attention; a study of its structure shows that it is of fundamental importance, as it proves to represent, in all probability, a stage in the evolution of the buccal armature of modern Ophiurids. The large mouth, which is guarded by exceptionally long teeth,

is bounded by five pairs of rods, and by the jaws with which these rods articulate at their inter-radial meeting place. The variable size of the oral angles in most specimens shows that the creature could undergo a considerable amount of distortion without breaking, and that the rods must therefore have articulated by loose sutures in the middle of the radius; indeed, the suture is occasionally visible as a groove in guttapercha casts taken from the better preserved specimens. The two halves of a jaw may also be separated. Inter-radially each rod overlaps the jaw abactinally, and thus comes into proximity with the corresponding region of one rod of the neighbouring oral angle. Each rod is marked out into regions by constrictions. According to our interpretation, these rods consist of a_1, a_2, and an abactinal crest of a_3, a_4, and possibly of a_5, these elements being fused end to end. It is possible that a_5 is merely overlapped by the distal end of the crest of a_4 (see text-figs. 2 and 4 D).

Text-fig. 4 D shows how the vertebral ossicles are related to the swellings of the rods. It follows from the foregoing statements that the ambulacral pieces of the first four pairs (or the halves of the first four vertebræ) diverge more or less from each other on each side of the radial line; a_1 and a_2 have also shifted upwards so that they lie upon, instead of beside, the corresponding adambulacral pieces, and a_3 has also shifted upwards, but to a less extent.

The above conclusions are based upon a study of the fossils and of the models constructed from serial sections of the fossils. On the ventral aspect of the fossil the inverted L-shaped ridges of the ventral surface of the ambulacral ossicles can be traced up to the oral angle in parallel series; at the angle, divergence of the members of the pairs of ossicles is seen to occur to a variable extent. The oral angle may be anything between 30° and 110° in different angles of the same specimen. When the fossil has a regular form these angles are between 30° and 40°; the divergence starts (that is the apex of the oral angle lies) between the members of the pair a_4; those of a_3 are distinctly divergent, and in front of a_3 no vertebræ can in general be distinguished on this aspect of the fossil. In some specimens, however, a slender rod is visible bounding each of the tentacle spaces t_1 and t_2 on their radial aspect; these rods we believe to be the radial margins of a_1 and a_2, they continue the curve started by the divergence of a_3 and a_4. In front of a_3 and continuing the line of the adambulacrals and articulating or fused with ad_3 is ad_2, which is simpler in form than the other adambulacrals and appears to carry no spines; at its other extremity it articulates with the jaws ad_1. Possibly its form is a survival of that which it originally had when the ambulacral pieces first moved upwards and outwards to their present position; it resembles the adambulacral pieces of the simpler and earlier Eophiura.

That the rods bounding the oral angle on the abactinal surface are formed of fused ambulacral ossicles is suggested by the following facts derived from a study of the fossils and models: The main part of the rod is composed of an abactinal crest which runs the whole length of a_3 and a_4, and of the radial border of a_5. This crest is

continued forwards over the tentacles to end upon the jaws. It is natural to expect the forward continuation to have an origin similar to that of the main part of the rod, and it is naturally in the neighbourhood of the tentacle spaces that we should look for the two missing ambulacral pairs (vertebræ), and, further, the inner margin of the rods continues, as already stated, the curve formed by the inner or radial surface of a_3 and a_4. That two vertebræ are represented in this remaining part of the rod is suggested by the fact that the space intervening between the anterior end of a_3, and the oral extremity of the rod, is just twice the length of a_3 or a_4; there are two tentacle spaces and adambulacral pieces underlying the piece in question, so that all the evidence there is goes to prove that the number of ambulacral and adambulacral pieces is equal in this ancient Brittlestar. Evidence from actual sutures is lacking, and also owing to the superposition of a_1 and a_2 upon the adambulacrals, the useful actinal L-shaped ridge no longer acts as a guide.

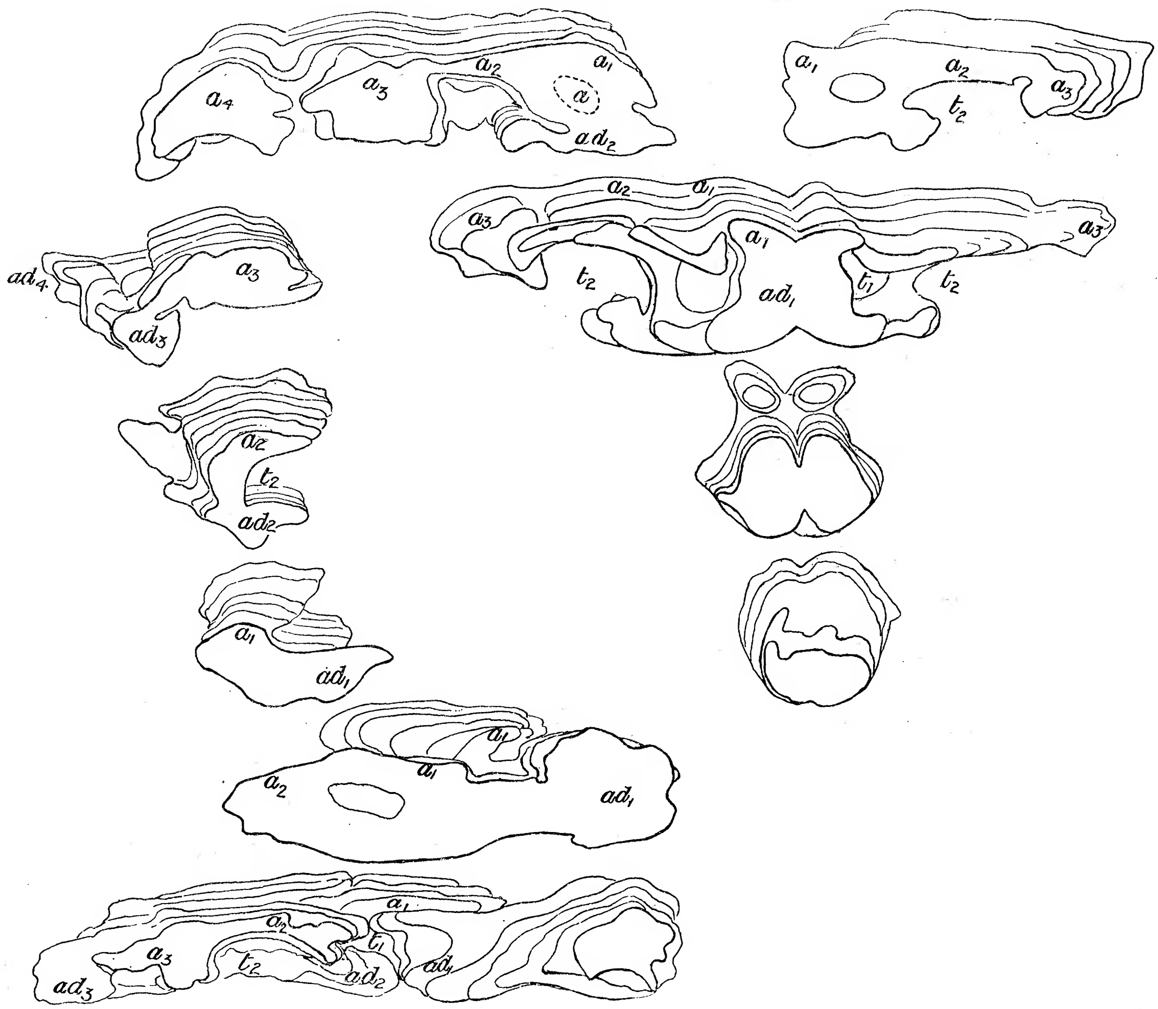

FIG. 1.—One oral angle of *Lapworthura miltoni* as represented by a model composed of vertical sections. Portions of the model are separated so as to show exposed to view at intervals the form of the sections composing it.

Nevertheless, in the complete absence of any evidence to the contrary, and considering the beautiful regularity of structure revealed by the models, there remains no great doubt that the full complement of vertebræ are present.

The first of the two models is built up of 265 vertical sections of the disc. The sections are at right angles to the long axis of one of the arms and consequently cut across the jaws at various angles. Of these sections some of the most instructive pass through the jaw almost at right angles to its length (fig. 1). Here we see a_1 lying above the first tentacle space and articulating with ad_1, but the sutures here, as elsewhere, are unfortunately obliterated. On the actinal surface, ad_2 is seen articulating with ad_1, and sending off an upward process by which it is connected with a_2; this process represents the stalk of the adambulacral, but is now upwardly instead of inwardly directed, owing to the altered relative position of a_2. On the other side of the gap left by the oral angle lies the other half of a_3, and its ambulacral articulating with it, the tentacle space for t_3 now lying on the outer side of the ambulacral piece. Behind this level we have parts of a_1, a_2, a_3, a_4 in succession, the sections running obliquely across the oral angle. Passing forwards along the border of the oral angle, a_3 with its ad_3 is succeeded by a piece containing the tentacle space of t_2, of which the roof is a_2 and the floor ad_2; a_2 is connected with ad_2 by its outer border and also by the upward process already seen which forms the partition between the two tentacle spaces t_1 and t_2. Passing the tentacle space t_1, we come to the jaw with a_1 well seen lying upon it, and separated from it by a suture both in this oral angle and the next one, reached after passing round the jaw. To trace the sections of this model further would involve too much repetition, and would only afford confirmatory evidence.

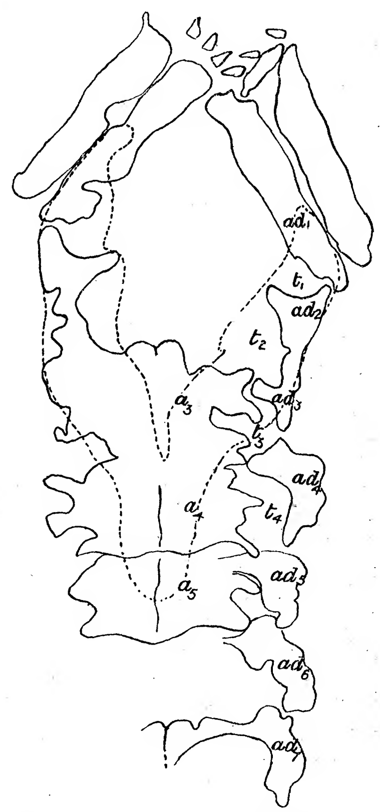

FIG. 2.—Superposed tracings of three horizontal sections of *Lapworthura miltoni*.

The second model is composed of 37 sections parallel to the surface of the disc passing through one of the oral angles (figs. 1 and 2, Plate 10). The angle of the mouth represented in this model measures 90°, and has been forced wider open than it would be in its natural position of rest. Owing to this fact, ad_3 is more concealed than is the case in some of the actual arms of any well-preserved specimen, ad_4 being the first adambulacral ossicle which is clearly visible; ad_3 is, however, to be found articulating with its neighbours on the under surface of the model, and underlying a_3 (fig. 2, Plate 10). A certain amount of shifting of this kind was, perhaps, possible during life. The perfect regularity of the adambulacral series when there is no

displacement of this kind is shown in text-fig. 2, which is obtained by superposition of tracings from photographs of Sections 10, 16, and 31.

The type of buccal armature here described in *Lapworthura miltoni* is in its main features precisely similar to that described by JAEKEL as occurring in Eophiura and Palæophiura, both from the Lower Silurian (D) of Bohemia. The chief differences are the fusion, end to end, of the halves of the abactinal portions of those ambulacral ossicles which diverge from their fellows in order to form the buccal fissures, the smaller number of these ossicles, and the greater vertical extent attained by the skeletal parts bounding the oral angle, particularly by a_3 and a_4. A further difference is the greater simplicity of ad_2 as compared with its fellows. In all these respects, and in the opposite arrangement of its ambulacral ossicles, Lapworthura shows a more advanced stage of development than the Lower Silurian forms, Eophiura and Palæophiura. In discussing the transition from the Eophiuran jaw to the jaws of modern forms, MACBRIDE says: "We may suppose that the gaping 'angles' of these old forms have, so to speak, healed up, except at their innermost portions." In Lapworthura we seem to be actually watching this process of healing up.

MACBRIDE also observes that in Eophiura: "The actual 'jaw' . . . . seems, as in modern forms, to consist only of the first adambulacral fused to the second ambulacral." In JAEKEL'S paper there is no statement to this effect, nor can we agree that his figures even suggest the loss of the first ambulacral ossicles.

Palæozoic Ophiuroidea other than Lapworthura.

It has already been stated that in its main features the structure of Lapworthura is typical of Silurian and Devonian Ophiuroidea, and that for this reason we propose to institute a new group, Protophiuroidea, to include all Silurian and Devonian Ophiuroidea with the exception of Eucladia and its ally, Euthemon. These genera were placed by one of us (2, 1899) in an order of Ophiuroidea, the Ophiocistia. BATHER (3, 1907) has recently made the very probable suggestion that the structures regarded as muscular arms are, in fact, gigantic scale-covered tube-feet. Thus the Ophiocistia, as far as we know them, agree with Ophiuroidea only in the possession of an actinal madreporite and of a buccal armature; these characters alone are not sufficient to justify the inclusion of these fossils in the Ophiuroidea. The Ophiocistia are, therefore, regarded as a class of Echinodermata, possibly allied to the Ophiuroidea.

The diagnostic characters of the group Protophiuroidea are, as already stated, (1) the completeness of the ambulacral series; (2) the meeting of the ambulacral series of adjacent arms on the abactinal surface of the jaws (ad_1); and (3) the absence of upper and under arm-plates. In respect of these three characters the structure of the Protophiuroidea is Asteroid in nature. The actinal position of the madreporite is also shared by some of the early Asteroidea, so that the sharp

limitation of the arms from the disc is the chief distinguishing character between the early Starfish and Brittlestars.

It is natural to ask what purpose was served by this outward and upward shift of the proximal ambulacral ossicles. Greater firmness of the buccal armature was obviously one advantage gained thereby. It is also clear that as long as the adambulacral ossicles formed a continuous series up to the jaws, and the vertebral ossicles were of no greater vertical extent than the adambulacral pieces, the latter would form an obstacle in the course of muscles running (like the external inter-radial muscles of the oral skeleton of modern forms) between the vertebræ of adjacent arms in the inter-radii behind the jaws.

Within the Protophiuroidea a gradual evolution can be traced. In the most primitive genera the ambulacral ossicles are neither completely alternate nor completely opposite. As examples of this most primitive structure Eophiura, Palæura, and Bohemura may be quoted. They are further characterised by the large number of ambulacral ossicles which bound the oral angles and by the absence of fusion with one another in a longitudinal series of these ossicles. For the forms with alternating ambulacral ossicles GREGORY (9) proposed the order Lysophiuræ. We were at first inclined to retain it as a division of the Protophiuroidea, referring the remaining members of the sub-order to a division Synophiuræ characterised by opposite ambulacral ossicles. But the state of knowledge at the present time hardly permits of this. For while it is certainly clear from JAEKEL'S work (11, see, for instance, his figs. 1 and 6) that in some of the simplest genera the ambulacral ossicles were not opposite, it is also certain that free opposite ambulacral ossicles are easily displaced either during life or after death, and it is difficult in some cases to be sure whether alternation is natural or due to displacement. We therefore think it wisest for the time merely to recognise the fact that there has been a progression within the Protophiuroidea from forms with free, partly alternating, ambulacral ossicles, on the one hand to forms with completely alternate ambulacral ossicles, and on the other to those in which these ossicles are opposite, at first free, afterwards having slight connections, and increasing in vertical extent, and that in both groups the buccal armature has advanced in complexity.

Through the kindness of Prof. T. McKENNY HUGHES we have had an opportunity of examining FORBES' *Protaster sedgwicki*, the type specimens of which are in the Sedgwick Museum. This species, together with a new species found by Dr. GROOM in the Middle Ordovician beds of Shropshire, for which we propose the name *Protaster groomi*, and the little *P. leptosoma* which we rename *Rhodostoma leptosoma*, form an interesting group for comparison with Lapworthura.

Protaster sedgwicki (Forbes) was described by FORBES in 1849 (8), and was found by him in Kirkby Moor Flags (Upper Ludlow) of Docker Park, Benson Knot. The type specimens include two casts, one of the actinal and one of the abactinal surface,

of an Ophiurid which agrees with FORBES' description, and which were figured by him, and, on a separate piece of rock, casts of the abactinal surface of a very different species having opposite ambulacral ossicles. It is rather badly preserved, but in those features which can be made out it resembles *Rhodostoma leptosoma*. GREGORY re-described *P. sedgwicki* in 1896 (9), and correctly described the L-shaped ridges, crossed by a groove, seen on the actinal aspect of the arms. It is curious that he does not mention the fact that the specimens labelled as type specimens belong to two different species, and that he gives a description of the ossicles at the distal end of the arms. The distal ends of the arms are broken off in the specimens having alternating ossicles; the specimens having opposite ambulacral ossicles agree neither with FORBES' nor GREGORY's description.

Protaster sedgwicki, as represented by the specimens figured by FORBES, is an Ophiurid with alternating ambulacral ossicles. The relative proportions of the disc and buccal armature contrast with those of Lapworthura; while the diameter of the disc in both species is 1·8 mm., that of the circle formed by the apices of the oral angles is 0·6 mm. in *P. sedgwicki* and 1·1 mm. in Lapworthura; on the other hand, the form of the ambulacral ossicles is closely similar in the two species. GREGORY has considered a Y-shaped appearance of some of the adambulacral ossicles near the mouth as one of the diagnostic characters of the genus, but we believe that this form, when it occurs, is simply due to the way in which the specimen is fractured. No spines are visible; FORBES, when he speaks of spines, seems to allude to the adambulacral plates. The scales of the disc are large and hexagonal. The first two adambulacral ossicles and the first three ambulacral ossicles are involved in the formation of the buccal armature. The first two adambulacral ossicles are fused with one another. The main bar bounding the oral angle appears to be formed by a great development of a_2, a piece which is probably a_1 lies parallel to this bar, from which it is marked off by a groove, and along its proximal margin, while a crest of a_3 lies alongside its distal margin, the greater part of the ossicle a_3 being overlapped by the large a_2.

The genus Protaster thus needs a fresh diagnosis, and from the evidence at our disposal we offer the following:—Protaster: Protophiuroidea with alternating ambulacral ossicles. The second ambulacral ossicles attain a large size and form the main ambulacral constituent of the buccal armature; they are elongated in a direction parallel to the oral angle (text-fig. 3). The first ambulacral ossicles are distinguishable as separate bars.

Protaster groomi agrees in all essential respects with *Protaster sedgwicki*, the same ossicles contributing to the buccal armature and a_1 being distinguishable as a separate bar. The greater complexity of form of the buccal armature, however, justifies the establishment of a new species for this form. As a full description of this species will be published by DR. GROOM, we confine ourselves to the statement that a_1 appears to have grown inwards towards the middle line from

its position on the abactinal side of the jaw (ad_1), and a large crest, which may be either wholly formed of a_2, or of a_2 and a_3, exists as in *P. sedgwicki*.

Rhodostoma leptosoma, from the same horizon as Lapworthura (*i.e.*, from the Lower Ludlow beds of Leintwardine), is represented by numerous specimens in the Oxford collection. One or two specimens presenting the actinal aspect are preserved in the original material. The whole calcareous skeleton is exceedingly slight and delicate. As in the two species of Protaster above described, the buccal armature is formed by abactinal crests of ambulacral ossicles which have elongated in a direction parallel to the borders of the oral angles. The first ambulacral ossicle, a_1, bounds the oral angle and is free from its successors; a_2 is the largest of the ambulacral ossicles contributing to the buccal armature, and in worn specimens it may appear to be the only one taking an important share in its formation. The laminæ of the adambulacrals are separated by a wide interval from the bodies of the vertebræ, the connecting pedicle, composed partly of their own stalk and partly of processes of the vertebræ, being long. It is no doubt owing to this fact that ad_2, instead of articulating at its distal end with ad_3, which could not afford it much support, has acquired a connection with a_3, thus giving extra firmness to the oral skeleton. The typical condition of the ambulacral ossicles is opposite; nevertheless, alternation may occur throughout the length of an arm and in all the arms of one specimen. The facts observed certainly suggest that this character is a variable one in the species. To obtain an idea of the form of the ambulacral ossicles, evidence from many specimens must be pieced together. They were apparently more or less rectangular, the members of a pair being in contact only at their anterior and posterior ends; their inner (radial) borders were thickened, appearing as a raised triangular area on the dorsal surface of the ossicle. The adambulacral pieces consist of a stalk lying in the plane of the actinal surface of the ossicle, and a spine-bearing bar, which curved back over the dorsal surface, so that the spines lay over the thinner regions of the ambulacral ossicles. On the actinal surface, the ambulacral ossicles show the usual L-shaped ridges.

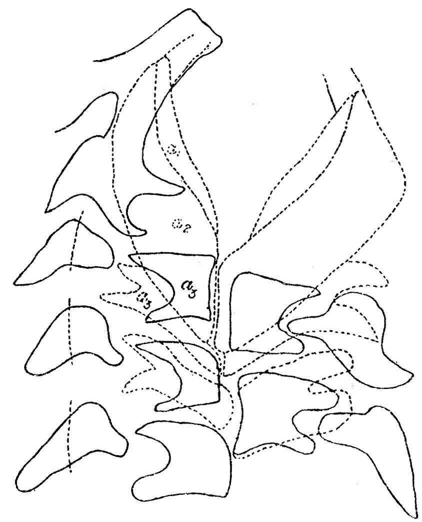

FIG. 3.—Buccal armature of *Protaster sedgwicki*: the figure is obtained by superposing camera lucida drawings of the dorsal and ventral aspects. Dorsal aspect dotted outline.

Protaster leptosoma (Forbes) was placed in the genus Sturtzura, created for it and *P. brisingoides* by GREGORY in 1898. CHAPMAN (6) restored *P. brisingoides*, the type species, to Protaster in 1907. Consequently, as BATHER (2) points out, the name Sturtzura becomes a synonym of Protaster. We propose to place the species in the new genus Rhodostoma, which is defined as follows:—Rhodostoma: Protophiuroidea

with either opposite or alternating ambulacral ossicles. Three ambulacral ossicles are modified as elements of the buccal armature, and are elongated in a direction parallel to the oral angles, thus giving to this part of the skeleton a petaloid appearance. It is to this that the name of the genus refers.

It will be seen that, according to the above interpretation, the buccal armature of the three species in question, while agreeing in the main features with that of Lapworthura, has, nevertheless, been developed in a somewhat different manner, but the difference is perhaps more apparent than real. In Lapworthura we have supposed that the bars bounding the oral angles have been formed by the fusion, end to end, of abactinal crests of the first four or five ambulacral ossicles, so that, if we could restore the original lines of fusion, they would be more or less transverse to the bar, instead of running along its length (fig. 4). This difference, however, will be seen to depend simply on the extent to which the component ossicles had elongated in a

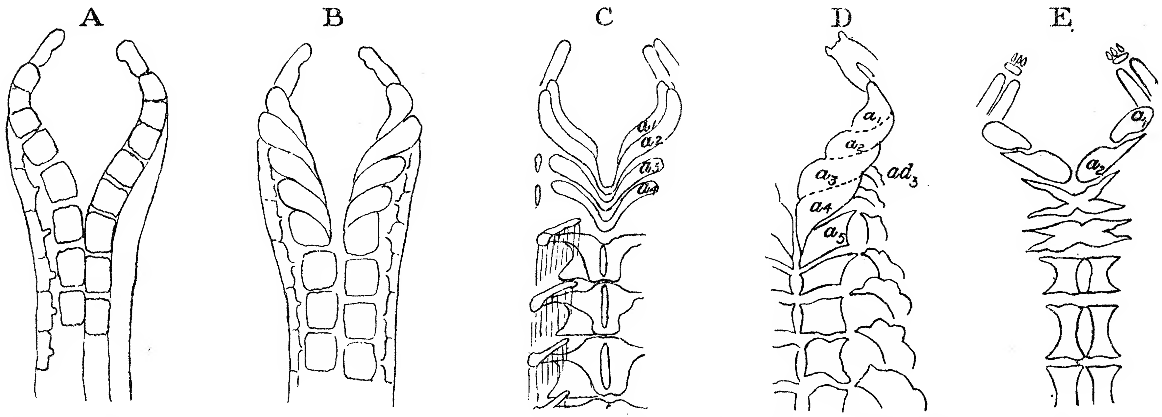

FIG. 4.—Series of schemes of buccal armatures of Palæozoic Ophiurids. A. Schematic figure of an early form based upon JAEKEL'S drawing of Eophiura. B. Hypothetical form in which the proximal ambulacral ossicles elongate, sending outgrowths towards the radial line. C. *Rhodostoma leptosoma.* D. *Lapworthura miltoni.* E. *Eoluidia decheni.*

direction oblique to their long axis previous to fusion with one another (when this fusion has occurred).

With the exception of Miospondylus, the most advanced genera are Furcaster, Eoluidia, Eospondylus. For these three genera STÜRTZ gives figures of the buccal armature which are almost interchangeable, and, indeed, the structures figured are remarkably similar. We believe that fig. 4 E gives the correct interpretation of the buccal armature in *Eoluidia decheni.* As in modern Ophiurids, a_2 forms the oral angle, but it is not yet indistinguishably fused with ad_1, and a_1 is still present. On the ventral surface of the arms, the familiar L-shaped ridges of the ambulacral ossicles are visible bounding an open groove. No trace of upper or under arm-plates is present.

Miospondylus rhenanus, of which a single specimen is known from the Lower Devonian of Bundenbach, has been described as having under-arm plates, a character

which was also attributed to Eoluidia and Eospondylus. The plates so named are visible in one arm only of the single specimen on its abactinal surface beyond the edge of the disc. This arm appears to have undergone rotation, so that, for the greater part of its length, its actino-lateral aspect is uppermost. Near the disc, where the rotation undergone is less, the so-called under arm-plates are clearly paired. What their real nature is remains problematic. Curious jointed structures, looking like jointed and flattened spines, are present on the lateral aspect of the arm and are named by STÜRTZ side shields.

Transition to Modern Forms: Nature of the Peristomial Plates.

It will be readily recognised that if the interpretation given in fig. 4 is correct, the step is not a long one from such a form as Eoluidia to a modern Brittlestar. The acquisition of upper and under arm-plates, the increase in vertical extent of the vertebræ, the complete fusion of ad_1 and a_2, comprise the necessary changes. That these changes had already taken place in the Lias is as shown by the sections and models which have been constructed by Miss WRIGHT (now Mrs. HALLAM, formerly of Somerville College, Oxford), of the Liassic Ophiurid, *Ophioderma egertoni*.

As is well known, LUDWIG's scheme of the homologies of the parts entering into the formation of the buccal armature of recent Ophiurids has met with general acceptance, with the exception of the homology of the peristomial plates, which, in the absence of evidence, is either denied or doubtfully accepted. Whatever may be the final decision upon this debatable point, we cannot fail to admire the insight which led LUDWIG, as early as 1878, to construct his well-known schemes of the Asteroid and Ophiurid mouth parts; by these, both types were reduced to a common plan, in which the ambulacral series of the neighbouring arms meet upon the abactinal surface of the jaws. The essence of his views has received a remarkable confirmation in the discovery of the structure of the Early Palæozoic Ophiuroidea, though he was almost certainly mistaken when he pressed the peristomial plates into service to fulfil the scheme. LYMAN, in 1882 (10), objected to LUDWIG's view that the peristomial plates were the homologues of the first pair of ambulacral ossicles, because, he said, "the plate is in no way connected with either of the mouth tentacles, and because it may be composed of one, two, or three pieces, or be altogether wanting."

In his valuable and now well-known paper, DR. ZUR STRASSEN brought forward, in 1901, further evidence against the homology. He considers that the morphological evidence is, of itself, almost sufficiently adverse; for when, as in the majority of species, peristomial plates are present, their number is not two, as LUDWIG's hypothesis would lead us to expect; but, further, when absent, their absence occurs not in the more specialised, but in the more primitive genera, in many species, for instance, of Ophiomusium, Ophioglypha, and Ophioplinthus. Palæontology completes this argument, for in *Ophioderma egertoni* from the Lias of

Lyme Regis, which agrees closely in skeletal structure with the more primitive of modern Zygophiuræ, peristomial plates are wanting. ZUR STRASSEN's embryological evidence taken alone was almost sufficient to prove that the peristomial plates are not ambulacral ossicles, for he shows that in *Amphiura squamata* ossicles, which are undoubtedly a_1, are still recognisable at a time when the peristomial plates are laid down. These are the "Löffelplättchen," which lie in the oral angles and afterwards disappear. At the same time, he describes certain other small ossicles, which he maintains are a pair of ambulacral ossicles, and a ventral plate. From this he concludes that not "2, but 3 segments take part in forming the oral region, of which the most anterior lacks lateral plates."

JAEKEL seems to follow ZUR STRASSEN in this view, but MACBRIDE points out that it requires that a number of tentacles have disappeared (11, p. 502). It also requires that in the first segment the lateral shields have disappeared, and in the second segment the under arm-plate. Further, though it cannot be objected that these ossicles are "in no way connected with the mouth tentacles," as LYMAN said of the peristomial plates, still they are associated with the tentacles of ZUR STRASSEN's second segment, while they are themselves, according to him, the ambulacral ossicles of his first segment.

In studying the development of *Amphiura squamata*, one of us found that these little ossicles are not constant in number; as a rule, there are two of them, each lying abactinally from the root of the first mouth tentacle. Either one of each pair, or both, have a downwardly directed elongation between the mouth tentacles reaching to the under arm-plate of the second segment. We have never observed the

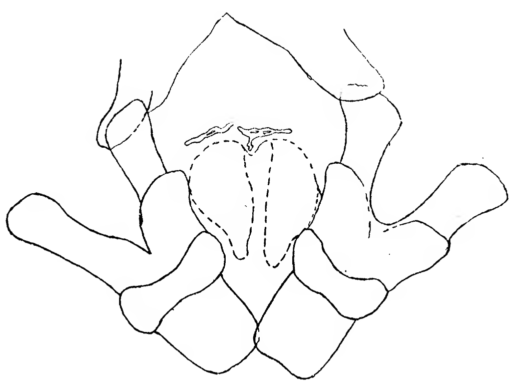

FIG. 5 (1).

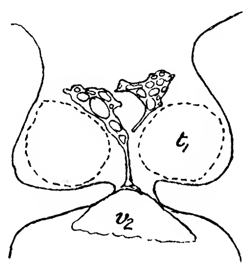

FIG. 5 (2).

FIG. 5.—(1) Horizontal section of an oral angle of *Amphiura squamata*, showing a pair of small ossicles (2) Vertical section of an oral angle of *Amphiura squamata*. One of the ossicles sends down a process reaching the under arm-plate v_2.

number 3, but in one and the same specimen we have seen a variation between 1 and 2 in the different oral angles. In *Ophiactis balli*, in the corresponding position, there is a single **T**-shaped ossicle.

Now, as is well known, a vertebra has a definite characteristic method of development, arising as a pair of simultaneously formed spicules between the terminal and the first-formed vertebra and abactinal to the main nerve trunks. The ossicles in the oral angles develop late, after the formation of a great part of the skeleton; if they were vertebral vestiges they should appear before all the other vertebræ. They are not more developed in their younger than in their final stage. If we assume them to be reduced vertebræ we are not at liberty to attribute their retardation to their vestigial nature, for LUDWIG'S "a_1," although they completely disappear at last, yet originate in their proper order.

It is true that LUDWIG accounts for the smaller size of a_1 at a time when a_1 and a_2 are the only ambulacral ossicles present, by stating that a_2 was the first to develop; but we have not found this to be the case. Rather a_1 owes its smaller size to its slower growth. Finally, the ossicles in the oral angles are ventral to the nerve trunks. These ossicles of *Amphiura squamata* are, as ZUR STRASSEN points out, represented in other forms by similarly placed but more substantial ossicles. We have observed them in microscopic sections of *Ophioglypha lepida* as hoop-like ossicles embracing the tentacles, articulating below with the under arm-plate of the second segment, above with ad_1, and we find that a precisely similar pair of ossicles is present in the Liassic species *Ophioderma egertoni*. There can be little doubt that they are "etwas neu erworbenes," as ZUR STRASSEN says, of the peristomial plates, and possibly they are the equivalent of an under arm-plate, the fact that they are double being due to their position. It should be pointed out that LUDWIG figures an under arm-plate in the vertical wall of the oral angle (9, Plate 3, fig. 1). Sometimes each of these little hoop-like plates is divided by a transverse suture. But too much value must not be attached to sutures, for they may be secondarily acquired. This is well shown in the case of the oral angle pieces. These pieces are formed, as is well known, by the fusion at an early stage of a_2 and ad_1, no line of demarcation being visible and processes of the two growing ossicles becoming inextricably entangled; later a transverse suture appears dividing this compound piece into two parts which are sometimes spoken of as a_2 and ad_1, a proceeding which is clearly inaccurate. This suture is doubtless adaptive and is already present in *Ophioderma egertoni*.

It is satisfactory to find that there is no conflict between the evidence, such as it is, from palæontology, embryology, and morphology as to the history of the buccal armature and arm-skeleton of Ophiuroidea.

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Note on the Construction of the Models. By Prof. Sollas.

Plaster models such as we have used in this study have many advantages over wax ones; they are more enduring, and can be readily reproduced. To obtain a plaster model is, however, by no means an easy problem; the obvious solution would seem to be to cast from a wax one, but if the latter be at all complicated, this is a task which even an expert will not undertake. The only way is to build up the plaster model in successive sheets, a method which is rendered possible by the fact that *plaster cast upon freshly-set plaster will adhere to it.* The steps in the process are as follows :—Tracings of the photographed sections are first made on transparent paper, and round each a rectangle is drawn to provide for exact registration. Sheets of wax are prepared of uniform thickness; placing one of these over a tracing the outline of the section is cut out with a fine pointed scalpel and the sides of the sheet are cut to correspond with the surrounding rectangle. When all the sections have been thus treated, the rectangular sheets of wax are superposed in order and the model, which exists now as a cavity in the wax, is examined to see if the registration is true. If this is found to be the case we may next proceed to reconstruct by casting. The first sheet in the series is attached to a plain sheet of wax which serves as base, plaster is then poured into the hollow of the section and allowed to set; directly afterwards the sheet with its contained plaster is placed in a specially constructed machine by which both sheet and plaster can be planed down to a definite thickness. The sheet is then removed from the machine and the next sheet in the series is registered upon it and attached, plaster is poured into the hollow, and wherever this rests on the plaster of the first sheet adherence takes place; the fresh surface is planed down, a third sheet added, and so on till the series is complete. It then only remains to remove the wax and set free the plaster model. This is an operation which requires great care. I have tried various methods, all of them depending on melting or melting and dissolving the wax; but none of them are quite satisfactory. The difficulty in all cases arises from softening of the wax before it melts, the weight of this softened wax pulling upon the slender processes of a model is often sufficient to break them.

The process is no doubt laborious, but it has the great advantage that the model, once obtained, may be handed over to an expert in making plaster casts, who will be able to take any number of copies from it.

To obtain sheets of wax of uniform thickness, the following method may be used: Two rectangular shallow tin dishes are constructed, one to fit inside the other. I find 50 mm. by 30 mm. a convenient size for the inner dish. The larger one is filled with water, to serve as a water bath, the inner with glycerine, and the whole is heated to above the melting point of the wax. A large quantity of melted wax is prepared, and a measured quantity, sufficient to give a sheet thicker than is required, is ladled out and poured over the hot glycerine. It is then allowed to cool and solidify. As it solidifies it must be cut away from the sides of the dish or it will be torn by contraction. The sheet is lifted from the glycerine by means of a false floor of perforated zinc, washed with water, and allowed to dry. It is then covered by a thin sheet of paper on each side, and run through a roller press (with hot rollers) such as is used by photographers for burnishing photographic prints. The interval between the rollers is adjustable, and uniform sheets of any desired thickness can be obtained in this way with a perfection not to be met with in those put upon the market by German firms.

The planing machine is a steel bed resting upon four millimetre screws at the corners, it works vertically up and down in a frame, the upper sides of which provide a sliding surface for the planing tool. The importance of planing to a measured thickness is due to the fact that it is impossible to attach* the sheets of wax one to another in such a manner as to secure perfect contact between them; a small but measurable interval always exists between the two opposed surfaces, and the sum of these intervals in a long series of sections would give a markedly greater thickness to the model than it ought to possess. By planing down after the addition of each sheet the model is kept to its true thickness.

* The simplest way to attach the sheets is to stick a hot needle through them, the melted wax makes a firm connection when solid; unfortunately, however, it intrudes by surface tension between the sheets, and thus establishes an interval.

DESCRIPTION OF THE PLATES.

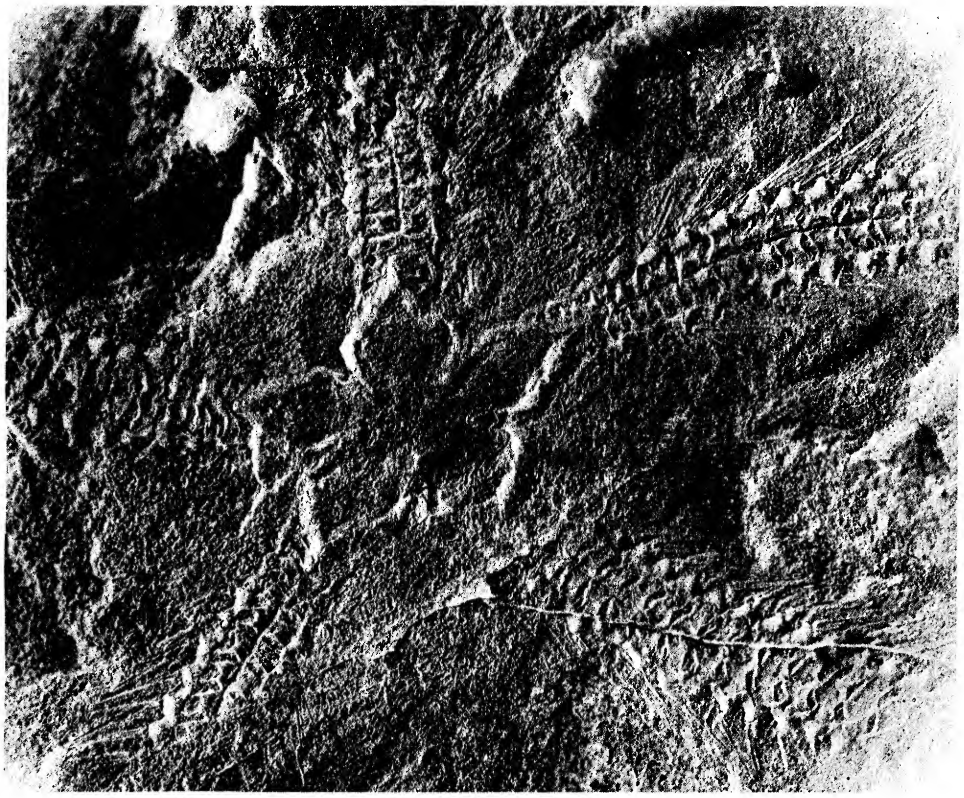
Plate 9.

1. *Lapworthura miltoni* (Salter), abactinal surface. × about 4.
2. *L. miltoni*, actinal surface. × about 5.
3. *Rhodostoma leptosoma*, abactinal surface. × about 4.
4. *R. leptosoma*, actinal surface. × about 5.

Plate 10.

1. Model composed of horizontal sections of one oral angle of *Lapworthura miltoni*, abactinal aspect. × 20.
2. Same model as in fig. 1, actinal aspect.
3. Models of skeleton of two arm segments, actinal and abactinal aspects. × 20.
4. Model composed of vertical sections of three complete oral angles.

1



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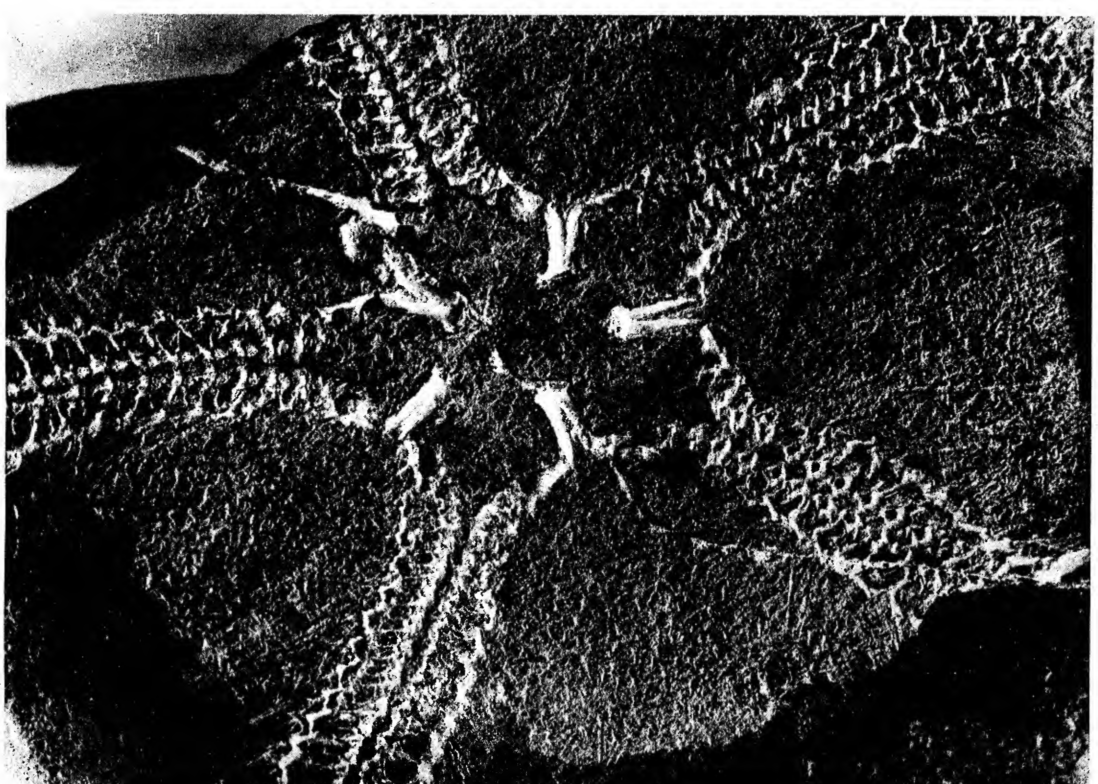

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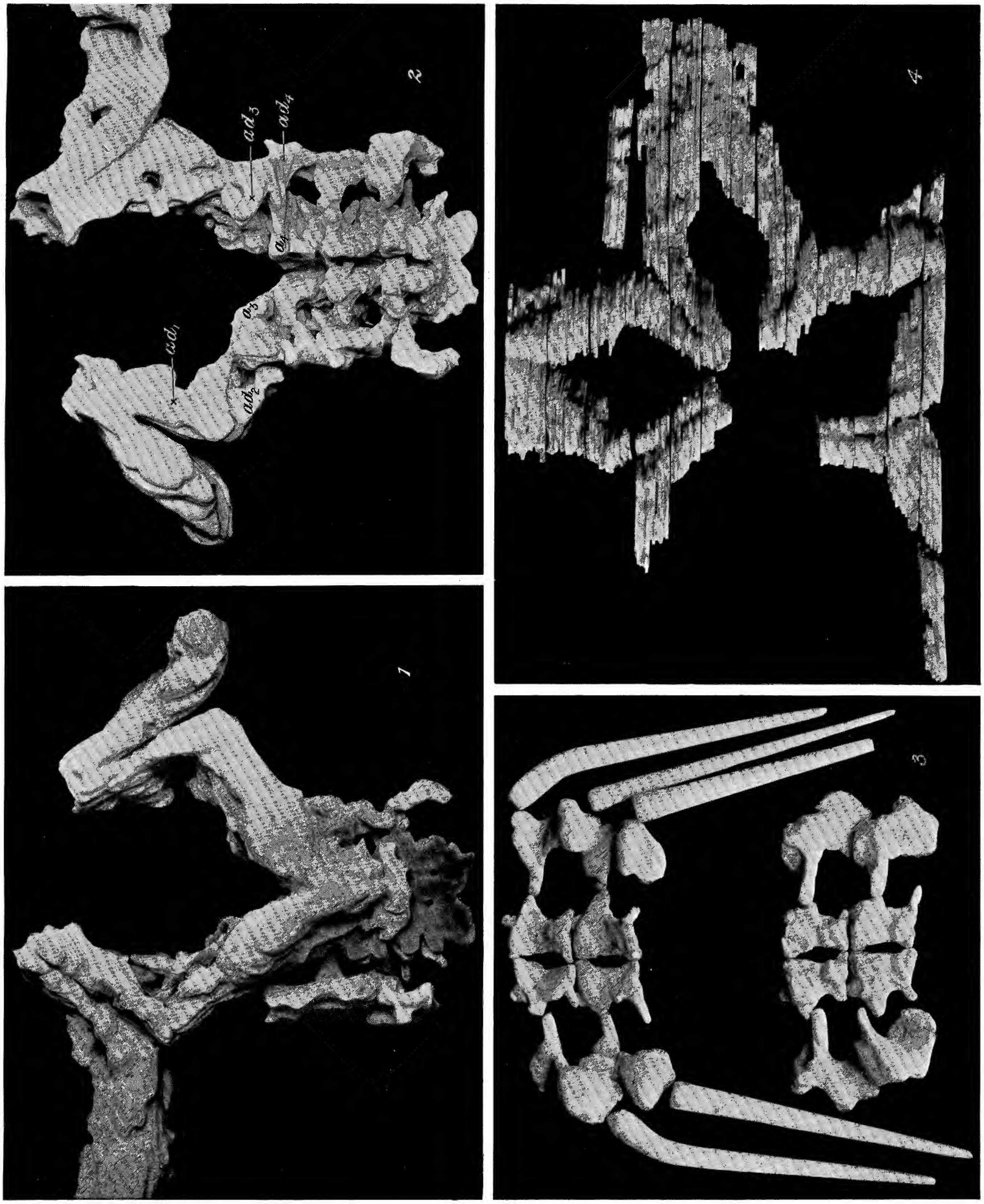

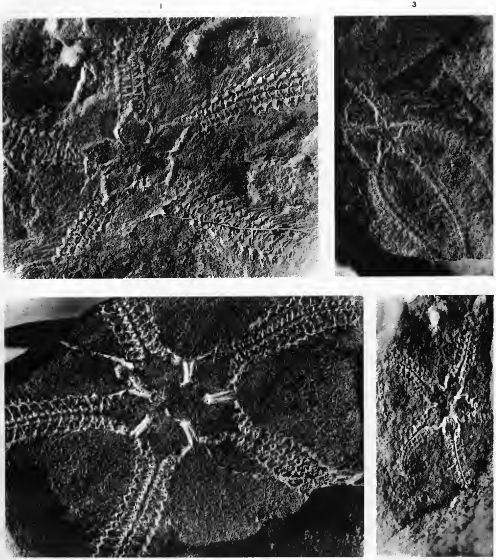

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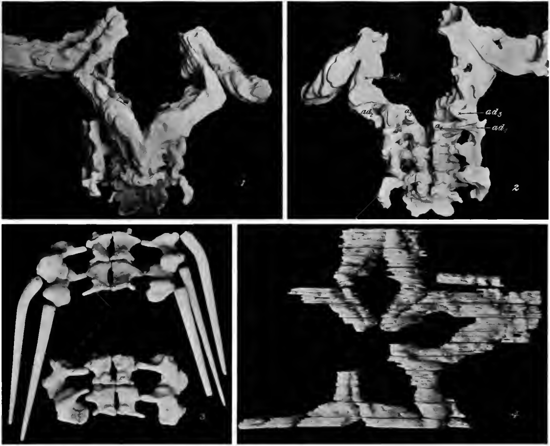

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